



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2018

Landscape configuration alters spatial arrangement of terrestrial-aquatic subsidies in headwater streams

Little, Chelsea J ; Altermatt, Florian

Abstract: Context: Freshwater ecosystems depend on surrounding terrestrial landscape for resources. Most important are terrestrial leaf litter subsidies, which differ depending on land use. We lack a good understanding of the variation of these inputs across spatial scales. **Objectives:** We sought to determine: (1) the relative importance of local versus catchment-level forestation for benthic leaf litter biomass in streams, (2) how landscape configuration alters these relationships, and (3) how land use affects the quality and diversity of leaf litter subsidies. **Methods:** We measured biomass and identity of benthic leaf litter in 121 reaches in 10 independent catchments seasonally over the course of a year. We assessed direct and indirect effects of forestation, reach position, and seasonality on leaf litter biomass using structural equation models, and assessed how leaf litter diversity varied with land use. **Results:** In catchments with forested headwaters, the degree of forestation and reach position in the catchment influenced benthic leaf litter biomass indirectly through local reach-scale forestation. In catchments where forest was only located down-stream, or with minimal forest, none of these factors influenced reach-level benthic leaf litter. Leaf litter diversity peaked in fall in all land use types, but was generally lowest in forested reaches. **Conclusions:** Not only habitat amount, but its location relative to other habitats is important for ecosystem function in the context of cross-ecosystem material flows. Here, lack of upstream forest altered spatial patterns of leaf litter storage. Studies with high spatiotemporal resolution may further reveal effects of landscape configuration on other ecosystems.

DOI: <https://doi.org/10.1007/s10980-018-0678-0>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-153775>

Journal Article

Accepted Version

Originally published at:

Little, Chelsea J; Altermatt, Florian (2018). Landscape configuration alters spatial arrangement of terrestrial-aquatic subsidies in headwater streams. *Landscape Ecology*, 33:1519-1531.

DOI: <https://doi.org/10.1007/s10980-018-0678-0>

Landscape configuration alters spatial arrangement of terrestrial-aquatic subsidies in headwater streams

Chelsea J. Little^{1,2} and Florian Altermatt^{1,2}

¹Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

²Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland

Author emails: Chelseajeane.little@eawag.ch, Florian.altermatt@eawag.ch

Corresponding Author: Chelsea J. Little

Department of Aquatic Ecology

Eawag: Swiss Federal Institute of Aquatic Science and Technology

Überlandstrasse 133

8600 Dübendorf, Switzerland

Telephone: +41 58 765 5786

E-mail: Chelseajeane.little@eawag.ch

ORCID: 0000-0003-2803-7465

Data Availability Statement

The data associated with this manuscript will be deposited at Dryad upon the manuscript's acceptance and publication. Data is currently available to editors and reviewers as supplementary material.

Acknowledgements

The authors sincerely thank the Kanton Thurgau Office of the Environment facilitating access to sampling sites, and all landowners whose property we crossed. We are also grateful to Pravin Ganesanandamoorthy, Elvira Mächler, and Simon Flückiger for help with fieldwork and laboratory work, and Katharina Kaelin and Rosi Sieber for assistance with parts of the GIS analysis. We thank two anonymous reviewers for their helpful comments. This project was funded by Swiss National Science Foundation grants PP00P3_150698 and PP00P3_179089.

Abstract

Context.

Freshwater ecosystems depend on surrounding terrestrial landscape for resources. Most important are terrestrial leaf litter subsidies, which differ depending on land use. We lack a good understanding of the variation of these inputs across spatial scales.

Objectives.

We sought to determine: (1) the relative importance of local vs. catchment-level forestation for benthic leaf litter biomass in streams, (2) how landscape configuration alters these relationships, and (3) how land use affects the quality and diversity of leaf litter subsidies.

Methods.

We measured biomass and identity of benthic leaf litter in 121 reaches in 10 independent catchments seasonally over the course of a year. We assessed direct and indirect effects of forestation, reach position, and seasonality on leaf litter biomass using structural equation models, and assessed how leaf litter diversity varied with land use.

Results.

In catchments with forested headwaters, the degree of forestation and reach position in the catchment influenced benthic leaf litter biomass indirectly through local reach-scale forestation. In catchments where forest was only located downstream, or with minimal forest, none of these factors influenced reach-level benthic leaf litter. Leaf litter diversity peaked in fall in all land use types, but was generally lowest in forested reaches.

Conclusions.

Not only habitat amount, but its location relative to other habitats is important for ecosystem function in the context of cross-ecosystem material flows. Here, lack of upstream forest altered spatial patterns of leaf litter storage. Studies with high spatiotemporal resolution may further reveal effects of landscape configuration on other ecosystems.

Keywords (4-6)

Land use, leaf litter, meta-ecosystem, resource subsidies, river network, terrestrial-aquatic linkages

Introduction

Freshwater ecosystems are intimately linked to their terrestrial surroundings. Embedded in a terrestrial matrix, streams, rivers, lakes, and ponds are defined by flows of resources and organisms to and from adjacent ecosystems. One major flux is the allochthonous input of carbon and nutrients (Fisher and Likens 1973; Chapin et al 2006; Gounand et al 2018). Headwater stream reaches are primarily heterotrophic (Marcarelli et al 2011). Compared to larger downstream reaches, they receive the bulk of terrestrial inputs, especially when considered per unit of streambed area, and this allochthonous material is then transported downstream, often after processing into fine particulate organic material by characteristic macroinvertebrate communities (Vannote et al 1980; Wipfli and Musslewhite 2004). Such headwater streams make up the vast majority of total global stream length (Downing et al 2012), have spatially varying water chemistry (Abbott et al 2018), and export high amounts of carbon to downstream reaches and water bodies despite their low flow volume (Wipfli et al 2007; Argerich et al 2016). They also harbor important biodiversity scattered throughout their small branches (Clarke et al 2008; Altermatt 2013), and can sustain high secondary production (Peterman et al 2008). Thus, it is important to understand allochthonous litter inputs in headwater streams and their effects on biodiversity and ecosystem function.

The diversity of terrestrial ecosystem types contribute different subsidies to freshwater ecosystems (Fuß et al 2017; Gounand et al 2018), with important consequences for communities and for ecosystem functioning. Among naturally-occurring types of land cover, forests, for example, contribute large amounts of leaf detritus and woody debris (Elosegi et al 2007), while grasslands can contribute less-recalcitrant grass materials and roots (Whiting et al 2011). Forests' contribution of woody debris is important because such debris is itself a resource subsidy, but also helps retain leaves and other terrestrial inputs, which can then be used by the freshwater food

web over a longer time period (Webster et al 1994; Allan 2004; Kominoski and Rosemond 2012). It is thus of no surprise that forest cover is well known to affect the community structure and richness of macroinvertebrates (Rios and Bailey 2006; Kaelin and Altermatt 2016; Ryo et al 2018). With decreasing forest cover, aquatic consumers derive more of their carbon from autochthonous sources (England and Rosemond 2004, Collins et al 2016), and the eventual loss of forest in a catchment and subsequent elimination of terrestrial detritus alters communities (Wallace et al 1997). Furthermore, forest cover is associated not just with the amount of leaf litter delivered to streams (Hagen et al 2010), but also its identity (i.e. in managed or logged vs. natural forests: Webster et al 1990; Lecerf et al 2005). The presence of preferred, high-quality detritus resources can have important effects on stream food webs and ecosystem processes (Marcarelli et al 2011), and species richness, evenness, and diversity of the leaf mixtures contribute to determining their breakdown rate, and thus how efficiently the subsidies are integrated into stream food webs (LeRoy and Marks 2006; Kominoski et al 2007; Swan et al 2009; Little and Altermatt 2018a). Thus, organic matter dynamics are a pathway through which land use change alters stream ecosystem function, as indicated by food webs and secondary production (Wallace et al 1997), community respiration (Young and Huryn 1999), and litter decomposition (Lecerf and Richardson 2010).

It has been posited that global change factors will have a larger effect on basal resources in streams and rivers when they occur in headwaters, which gather more allochthonous inputs and export them downstream, than if they occur in downstream reaches, where autochthonous production is more prominent (Kominoski and Rosemond 2012). This is because the export of partially-decomposed allochthonous material and litter-derived dissolved organic carbon from upstream to downstream reaches is so important in characterizing downstream ecosystems (Vannote et al 1980; Wipfli et al 2007). As a result, reduction of subsidies in headwaters could

also alter downstream ecosystems (Meyer et al 1998; Harvey et al 2017). While some previous research has considered the effect of landscape composition on subsidies to freshwater ecosystems (England and Rosemond 2004), the effect of landscape configuration, or how these land use types are arranged in space, remains unexamined. For instance, while models of how ecosystem services are affected by fragmentation are increasingly spatially explicit, they often consider fragment size in a random or systematic pattern (i.e., Mitchell et al 2015) rather than position in the landscape per se. Yet because land cover types are not distributed randomly across landscapes, but are associated with topography and geomorphology, this is potentially important. In one example, streams with intense land use upstream vs. downstream had different patterns of macroinvertebrate richness along the length of their catchments (Niyogi et al 2007).

Here, we worked in ten independent stream catchments on the shores of Lake Constance in Eastern Switzerland (Figure 1). This region is characterized by a mixture of land uses, from forests (primarily managed for timber, but also in some natural reserves) to agriculture of varying intensities, from pasture to fruit and vegetable farming. In the last half century, the many small villages of the region have grown in size, tourism has boomed leading to more campgrounds, and parts of the region have also industrialized (Schmieder 2004). Looking forward, the area is projected to see a change in the types of agriculture being practiced, as well as further urbanization (Price et al 2015). Thus, the catchments already have a wide variety of landscape compositions and configurations, and human impacts are only likely to increase in the future.

We sampled 121 reaches across these ten catchments to determine effects of land use and landscape configuration on standing stock and diversity of allochthonous leaf litter available in streams. We hypothesized that in these stream catchments: (1) different spatial arrangements of land use and land cover types will show different patterns in the relative importance of local vs. upstream contributions of terrestrial subsidies; (2) the standing crop of terrestrial leaf litter in

stream reaches will vary seasonally, with different temporal patterns depending on position in the stream catchment; and (3) the diversity of leaf detritus in stream reaches will vary with land use and season. Testing these hypotheses will allow us to understand both stream ecosystem function in the landscapes that currently surround us, and what the effects of changing land use and management practices might have on streams.

Methods

Site selection and benthic leaf litter sampling

Ten headwater stream catchments on the Swiss side of Lake Constance were selected for study (overview see Figure 1, for details on the catchments see also Appendix I, Figure S1, Table S1), with streams between 2.75 and 5 kilometers in length and their catchments covering between 115 to 453 hectares. Catchments were chosen due to prior knowledge of dominant macroinvertebrate communities in some of them (Altermatt et al 2016), and all catchments were concurrently surveyed for macroinvertebrates (Little and Altermatt 2018b). The catchments were also chosen in part to ensure that only minimal sections of the watercourses were buried in culverts, both to ease sampling and because such modifications strongly affect the abiotic and biotic characters of a stream. Three catchments were primarily forested downstream, with upstream reaches surrounded by anthropogenic land use types, predominantly agricultural use (designated “*downstream forest*”); three catchments had large tracts of forest near the headwaters, but varying non-forested land use types downstream near the lake, which were either mostly urbanized or agricultural (“*upstream forest*”); and three catchments had very minimal forest, distributed in small fragments in varying parts of the catchment (“*not forested*”). One additional catchment was almost completely forested (“*all forested*”).

In each catchment, streams were divided into 250 meter segments along the main stem, starting from the lake outlet in an upstream direction. Side stems less than 450 meters in total length were counted as single segments, while tributaries greater than this length were further divided into 250 meter segments beginning from the confluence with the main stem. Each stream segment was visited in late April or early May 2015, and a sampling point was established within the segment where habitat and stream flow was as representative as possible of the whole length of the segment, except in a few cases where entire segments were inaccessible due to extreme terrain or private property restrictions. This resulted in 121 total sampling points distributed with a range of nine to 15 sampling points per catchment. Individual stream catchments and their designation into different configuration categories are shown in Appendix I, Figures S2-S8.

Points were visited four times for a year, starting with the April/May 2015 visits when the points were established. Subsequent visits were during July 2015, October/November 2015, and January 2016. The fall sampling visits occurred between days of the year 292 and 310, which were during the peak autumn leaf drop as measured by leaf litter traps (Appendix II, Figure S9); leaf drop had declined to near-zero baseline levels by the winter sampling visit so that leaves entering the stream would have arrived primarily by lateral transport. The actual sampling points were not repeated exactly, but were repeated to within a 10 meter stretch of the study reach. At each visit, stream width was measured and benthic leaf litter was collected from a defined area of the stream section, typically a 0.2 x 0.2 m square area. In this study, we did not quantify standing stock biomass of woody debris, although we did estimate the area of substrate it covered in each stream reach (Appendix II, Figure S10). When brought back to the lab, leaves were sorted to the genus or species level, then dried in a 60 °C oven for 48 hours. In order to estimate the total amount of benthic leaf litter residing in that stream reach, the area sampled was multiplied by the fraction of area it represented of the 1 m long section of the stream, depending on stream width,

thus giving us amount and type of leaf litter in each of the focal 1 m long stream segments distributed throughout the 10 stream networks.

Land use assessment

Spatial information was extracted from the catchments using ArcGIS version 10.2.2 (ESRI, Redlands, California, USA). Data about the watercourses were extracted from the Swiss national 1:25,000 scale water network (Swisstopo 2007), which was used to determine the distance of each sampling point from the stream's outlet into Lake Constance. The elevation of each sampling point was determined by overlaying the stream network on a digital elevation model accurate to within two meters (Swisstopo 2003).

Land cover within the catchments was primarily classified from the CORINE land cover (2012) European Environment Agency (EEA) land-use classification (Bossard et al 2000), produced from Indian Remote Sensing (IRS) P6 LISS III and RapidEye imagery with a Minimal Mapping Unit of 25 hectares and positional accuracy of, at a minimum, 100 meters. To add additional detail to CORINE's agricultural classification, we also determined the area of vine and orchard fruit cultivation from the Swiss national 1:25,000 scale vector map (Swisstopo 2010). After merging these two data sources, land cover within the catchments fell into nine categories: discontinuous urban fabric, industrial or commercial units, non-irrigated arable land, complex cultivation patterns, fruit orchards and vine cultivation, broad-leaved forest, mixed forest, inland marshes, and water bodies. The area of land falling into each land use category was calculated for each study catchment in total, as well as for a 50-meter radius circular area surrounding each individual sampling point. As well as a quantitative measure of land use types in this radius, the circular area was used to qualitatively classify the most prevalent land use type at the sampling point into forest, orchard, other agriculture, or urban/suburban.

Statistical analysis

All statistical analyses were done in R version 3.3.2 (R Core Team, Vienna, Austria, 2016). The direct and indirect effects of land use on the total amount of benthic leaf litter in stream reaches (g/m^2) was modeled using structural equation models in the ‘lavaan’ package version 0.5-23.1097 (Rosseel 2012). All variables were standardized in order to allow direct comparisons between their effects. Separate models were assessed for the “*downstream forest*” ($n=138$ observations used), “*upstream forest*” ($n=117$), and “*not forested*” ($n=134$) datasets. For each model, proportion of forest in the point’s 50 m buffer was modeled as a function of catchment proportion forest and distance from outlet, and the amount of benthic leaf litter was modeled as a function of catchment proportion forest, point proportion forest, distance from outlet, and sampling bout (April, July, October, or January). Model fit was assessed using chi-squared statistics and models were considered a good fit if p-values associated with the chi-squared were >0.05 , and the root mean square error of approximation (RMSEA) was <0.05 . To assess the significance of each path in the structural equation model, z-statistics were used and only paths with a significance of $p < 0.05$ were considered important. Indirect effects were only considered important, and calculated as the product of effect sizes of the two path segments, if both segments were significant at $p < 0.05$. Parameter estimates are reported based on complete standardization of all variables in the model. The same model was also applied to the “*all forested*” ($n=48$), with the modification that the catchment proportion forest was excluded from the structural equation model as there was no variance since there was only one catchment in the dataset.

To examine the relationship between land use type, season, and benthic leaf litter diversity, we transformed the leaf litter species data from each sample into proportional

abundances. For each sampling point, we used the land use type in the 50 m buffer to determine a categorical grouping into four factor levels: forest (including mixed and broadleaf forest), orchards (areas with fruit orchards and vine cultivation), other agriculture (including non-irrigated arable land and complex cultivation patterns), and urban-suburban (including discontinuous urban fabric and industrial or commercial units). Then, we performed a distance-based redundancy analysis, dbRDA (Legendre and Anderson 1999) using the capscale function of the ‘vegan’ package, version 2.4-1 (Oksanen et al 2012). This constrained ordination approach, in contrast to an unconstrained ordination, allowed us to directly examine our hypothesis that the community composition of benthic leaf litter in different stream reaches would be related to land use type surrounding the reach. Distance-based RDA uses non-Euclidean distance measures, in our case Bray-Curtis distance, to represent ecological distance, which is a better fit for species abundance data than Euclidean distance measures (Faith et al 1987). Based on our sampling design, in our dbRDA analysis we considered season and land use type to be fixed factors, and catchment identity to be a conditional factor (analogous to a random factor in linear models, explaining some variation in the response variable but not of experimental interest).

The first capscale axis of the dbRDA was extracted as a proxy of benthic leaf litter diversity. Having done so, we applied the same structural equation model described above for benthic leaf litter abundance to benthic leaf litter diversity. Because we hypothesized that forest/land use type, not just the amount of forest, would determine the diversity of leaf litter subsidies to streams, we also analyzed diversity (CAP1 axis) and species richness of benthic leaf litter using linear models with surrounding land use type and season as interacting fixed effects.

Results

Leaf litter biomass

Factors influencing total benthic leaf litter availability varied with landscape configuration. Structural equation models had moderate fit for data from catchments with forest primarily upstream ($\chi^2 = 3.825$, $p = 0.28$, RMSEA = 0.048). Here, forest cover at a sampling point mediated indirect effects forest cover at the catchment level and distance from the outlet on benthic leaf litter (Fig. 2a). Models had good fit for data from catchments with forest primarily downstream ($\chi^2 = 0.13$, $p = 0.99$, RMSEA < 0.001) and from catchments with minimal forest ($\chi^2 = 1.76$, $p = 0.63$, RMSEA < 0.001). In catchments with forests primarily downstream (Fig. 2b), there were no indirect effects: while forest cover at the sampling point was negatively associated with the sampling point's distance from the outlet (direct effect = -0.17, $p = 0.05$), neither had a significant causal effect on benthic leaf litter availability. In catchments with minimal forest (Fig. 2c), forest cover at the sampling point was positively associated with distance from the outlet (direct effect = 0.29, $p < 0.001$), but again neither of these two factors had a significant causal effect on benthic leaf litter availability. In all three types of landscape configurations examined, there was greater leaf litter availability in fall ($0.37 < \text{direct effect} < 0.41$, all $p < 0.001$) and winter ($0.28 < \text{direct effect} < 0.35$, all $p < 0.015$) compared to in summer (Fig. 3). In the catchment which was nearly completely forested, the structural equation model had a good fit ($\chi^2 = 0.36$, $p = 0.95$, RMSEA < 0.001) and while the proportion of forest in a sampling point's 50 meter buffer was positively associated with distance from the stream outlet (direct effect = 0.67, $p < 0.001$), none of the factors – including season – had significant direct or indirect effects on benthic leaf litter availability (Appendix II, Figure S11).

Leaf litter diversity

The dbRDA ordination showed that benthic leaf litter community composition was constrained by land use type. 10.8 % of the inertia (analogous to variance) was attributed to the

constrained factors, land use type and season, while 14.8 % was attributed to the catchment identity. A permutation test showed that the CAP1 axis, which explained 7.6% of the variation, was a significant predictor of community composition ($F_{1,395} = 34.521$, $p = 0.001$), as were the CAP2 (3.1% of variation explained; $F_{1,395} = 13.906$, $p = 0.001$), CAP3 (1.4% of variation explained; $F_{1,395} = 6.223$, $p = 0.001$), and CAP4 (0.6% of variation explained; $F_{1,395} = 2.783$, $p = 0.02$) axes. Furthermore, both season ($F_{3,395} = 20.127$, $p = 0.001$) and land use type ($F_{3,395} = 3.957$, $p = 0.001$) were significant in explaining variation in leaf litter composition (Fig. 4).

The CAP1 axis had a high negative loading for beech leaves, while near-zero and positive values were associated with greater species diversity (Fig. 5a). In the structural equation models, proportion of catchment forestation was never significantly associated, either directly or indirectly, with the CAP1 diversity metric in any landscape type. In all landscape types, diversity was highest in fall, and depending on landscape type diversity was directly associated with either proportion of forest at the sampling point, or the sampling point's distance to the outlet (Appendix II, Figure S12). Linear models indicated that seasonality interacted with land use type: diversity of leaf litter varied with both land use type and season when measured with two different metrics. Value of the CAP1 axis from the dbRDA ordination varied with a significant interaction between surrounding land use type and season ($F_{9,395} = 2.65$, $p = 0.005$; Fig. 5b). Number of species in a sample varied significantly with land use type ($F_{3,395} = 17.92$, $p < 0.001$) and season ($F_{1,395} = 34.54$, $p < 0.001$), but the two factors did not have a significant interaction (Fig. 5c). The importance of the interaction in the capscale diversity proxy but not in the species number indicates that there are differences in species identity between samples even when the number of species does not vary.

Discussion

We found that in fragmented landscapes with mosaics of forests and anthropogenic land use types, both local land use and landscape configuration affect terrestrial leaf litter subsidies to headwater streams. Higher forestation in a catchment both directly and indirectly increased the diversity of leaf litter subsidies to streams, yet throughout most of the year, sampling points in forested reaches had lower diversity of benthic leaf litter than reaches in different land use types. This is unsurprising as central European forests are heavily beech-dominated, including those in Switzerland (Heiri et al 2009), whereas land use is associated with differences in riparian vegetation (Webster et al 1990; Aguiar et al 2018). The amount of leaf litter subsidies available in stream reaches depended not just on local land use, but also on the spatial configuration of land use types. Greater forestation at the catchment level only affected benthic leaf litter availability in streams if that forest was located in the upstream portion of the catchment. These patterns have important implications for stream ecosystems, which are usually net heterotrophic and depend on allochthonous resources to accompany autochthonous production.

It is difficult to obtain a comprehensive budget of leaf litter subsidies for a variety of reasons, including high spatio-temporal variability in leaf shedding, transport, and processing. While we estimated the standing crop of leaf litter available in streams, we do not know precise inputs of leaf litter to streams (although, see Appendix II, Figure S9), processing rates by macroinvertebrate and microbial communities in stream reaches, or how much leaf litter was swept downstream without ever being processed. Thus, we find only a snapshot of leaf litter availability in space and time. Two reaches may have the same standing crop even if one reach has higher inputs but also higher processing and export, and another reach has fewer inputs but also lower processing rate of these subsidies. This has the potential to alter some conclusions: for example, it is possible that in forested headwater streams the leaf litter input is actually moderately diverse because riparian vegetation differs from that of the beech-dominated forest

itself, but that these higher-quality resources are consumed by macroinvertebrates, microbes, and fungi more quickly upon entering the stream (i.e., Swan and Palmer 2006) and thus disappeared before they could be noted in our benthic leaf litter surveys. However, the fact that diversity of benthic leaf litter in forested reaches was lower than in other reaches even during fall leaf drop suggests that even if this mechanism is occurring, there is still some substantial difference in the diversity of leaf litter subsidies from different land use types. In many of our upstream reaches stream width was well under one meter, and conditions at the edges of such small streams are not as different or typically riparian as around larger stream reaches. Furthermore, riparian vegetation is generally less diverse in headwater than downstream catchments (Kuglerová et al 2016), which matches the pattern we found.

Despite the challenges in comprehensively estimating leaf litter inputs to streams, our study design provided unprecedented spatiotemporal detail and spanned considerable variation in both catchment land use and configuration. We worked in 10 catchments ranging from zero percent forest land use to 85% forested. Previous work has shown that over a range of 82–96% forestation, having more forest in a catchment increased the standing crop of coarse particulate organic matter in autumn (England and Rosemond 2004). However, that study found no relationship between catchment forestation and coarse particulate organic matter in spring, and also aggregated all data at a sampling timepoint into one measurement per stream. In our analysis, we not only covered a more realistic and larger range of landscape compositions and configurations, but were able to also assess how leaf litter availability varied longitudinally along the length of a catchment. In catchments with forest upstream, both the proportion of forest in the catchment and a reach's position in relation on the headwaters-to-outlet continuum determined the availability of leaf litter. That these factors were not important to the availability of benthic

leaf litter when forest was located downstream or removed completely, suggests that the factors driving leaf litter subsidy availability downstream are independent of major landscape features.

Our findings have important implications for the functioning of stream and river ecosystems, especially in the context of ongoing land use changes and fragmentation.

Allochthonous inputs are typically highest in headwater reaches, and are exported downstream both in their whole form and after processing into fine particulate organic matter, which is a resource for the differently-structured macroinvertebrate communities downstream (Vannote et al 1980). Even seemingly moderate changes in land use can affect this pattern: for example, natural forests and regenerating, previously-logged forests have different magnitudes and types of leaf litter inputs to streams (Webster et al 1990), and differences in leaf inputs between forested and agricultural reaches may be even larger (Hagen et al 2010). Reducing terrestrial subsidies in headwaters could thus not only reduce productivity of upstream reaches, but also potentially the productivity of downstream reaches as less detritus is processed into fine particulates.

Furthermore, deforestation in headwater reaches may change the biotic community through other mechanisms. For example removing shading vegetation may increase the potential for autochthonous production as well as alter stream temperature, and land use may alter water chemistry and contribute contaminants or excess nutrients (Sponseller et al 2001). When this is the case, the biotic community may change to the extent that it could no longer efficiently process allochthonous subsidies even if they were provided (Hagen et al 2006). Indeed, work in experimental microcosms suggests that this alteration would be propagated downstream because changes in upstream biotic community structure affect subsidy export and thus downstream population and community dynamics (Harvey et al 2017).

Maintaining tree cover in riparian zones has become a recommended tool to maintain terrestrial subsidies, structural features in stream channels, water chemistry, temperature, and

sediment trapping (Naiman et al 1993; Miltner et al 2004; Sweeney and Newbold 2014). Yet if riparian vegetation has a predominantly local effect on organic material in streams (Johnson and Covich 1997), such riparian buffers may be insufficient to mediate catchment-scale impacts of land use changes (Snyder et al 2003). And while leaf litter is not the only allochthonous carbon source supporting stream food webs, other resources such as dissolved organic carbon may be affected by the same land use changes that alter leaf litter subsidies (Allan 2004). Alternatively, maintaining upstream forested reaches has been identified as a strategy to maintain biodiversity refugia for recolonization of macroinvertebrates to impacted downstream reaches (Orlinskiy et al 2015), and could likewise be essential to maintain these terrestrial subsidy delivery at the whole-catchment scale.

Conclusion

Altering allochthonous subsidy delivery to upstream reaches could alter the core assumptions about how organic material is distributed through catchments. While land use change affects some aspects of terrestrial leaf litter subsidies, such as diversity of leaf litter, no matter where it occurs, we found that the spatial configuration of land use types in a catchment alters the way that the standing crop of benthic leaf litter is distributed through catchments. Because this results in a separation of benthic leaf litter dynamics from purely local land use and vegetation, the spatial patterns we identified may also indicate that riparian buffers are insufficient to maintain litter subsidies at the catchment level. Maintaining forested headwater areas may be essential to preserve characteristic spatial dynamics of organic matter in streams.

References

Abbott BW, Gruau G, Zarnetske JP, et al (2018) Unexpected spatial stability of water chemistry

- 396 in headwater stream networks. *Ecol Lett* 21:296–308. doi: 10.1111/ele.12897
- 397 Aguiar FC, Segurado P, Martins MJ, et al (2018) The abundance and distribution of guilds of
 398 riparian woody plants change in response to land use and flow regulation. *J Appl Ecol* 1–14.
 399 doi: 10.1111/1365-2664.13110
- 400 Allan JD (2004) Influence of land use and landscape setting on the ecological status of rivers.
 401 *Annu Rev Ecol Evol Syst* 35:257–284. doi: 10.1146/annurev.ecolsys.35.120202.110122
- 402 Altermatt F (2013) Diversity in riverine metacommunities: a network perspective. *Aquat Ecol*
 403 47:365–377. doi: 10.1007/s10452-013-9450-3
- 404 Altermatt F, Alther R, Mächler E (2016) Spatial patterns of genetic diversity, community
 405 composition and occurrence of native and non-native amphipods in naturally replicated
 406 tributary streams. *BMC Ecol* 16:23. doi: 10.1186/s12898-016-0079-7
- 407 Argerich A, Haggerty R, Johnson SL, et al (2016) Comprehensive multiyear carbon budget of a
 408 temperate headwater stream. *J Geophys Res* 121:1306–1315. doi: 10.1002/2015JG003050
- 409 Bossard M, Feranec J, Otahel J (2000) The revised and supplemented Corine land cover
 410 nomenclature. European environment agency, Copenhagen, Denmark
- 411 Chapin FS, Woodwell GM, Randerson JT, et al (2006) Reconciling carbon-cycle concepts,
 412 terminology, and methods. *Ecosystems* 9:1041–1050. doi: 10.1007/s10021-005-0105-7
- 413 Clarke A, MacNally R, Bond N, Lake PS (2008) Macroinvertebrate diversity in headwater
 414 streams: A review. *Freshw Biol* 53:1707–1721. doi: 10.1111/j.1365-2427.2008.02041.x
- 415 Collins, SM, Kohler, TJ, Thomas, SA, Fetzer, WW, Flecker, AS (2016) The importance of

- 416 terrestrial subsidies in stream food webs varies along a stream size gradient. *Oikos* 125:674–685.
 417 doi: 10.1111/oik.02713
- 418 Downing JA, Cole JJ, Duarte CM, et al (2012) Global abundance and size distribution of streams
 419 and rivers. *Int Waters* 2:229–236. doi: 10.5268/IW-2.4.502
- 420 Elosegi A, Diez J, Pozo J (2007) Contribution of dead wood to the carbon flux in forested
 421 streams. *Earth Surf Process Landforms* 32:1219–1228. doi: 10.1002/esp
- 422 England LE, Rosemond AD (2004) Small reductions in forest cover weaken terrestrial-aquatic
 423 linkages in headwater streams. *Freshw Biol* 49:721–734. doi: 10.1111/j.1365-
 424 2427.2004.01219.x
- 425 Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of
 426 ecological distance. *Vegetatio* 69:57–68. doi: 10.1007/BF00038687
- 427 Fisher SG, Likens GE (1973) Energy Flow in Bear Brook, New Hampshire: An Integrative
 428 Approach to Stream Ecosystem Metabolism. *Ecol Monogr* 43:421–439. doi:
 429 10.2307/1942301
- 430 Fuß T, Behounek B, Ulseth AJ, Singer GA (2017) Land use controls stream ecosystem
 431 metabolism by shifting dissolved organic matter and nutrient regimes. *Freshw Biol* 62:582–
 432 599. doi: 10.1111/fwb.12887
- 433 Gounand I, Little CJ, Harvey E, Altermatt F (2018) Worldwide cross-ecosystem carbon subsidies
 434 and their contribution to ecosystem functioning. *bioRxiv* 271809. doi: 10.1101/271809
- 435 Hagen AEM, Webster JR, Benfield EF, et al (2006) Are leaf breakdown rates a useful measure of
 436 stream integrity along an agricultural landuse gradient? *J North Am Benthol Soc* 25:330–

- 437 343. doi: 10.1899/0887-3593(2006)25[330:ALBRAU]2.0.CO;2
- 438 Hagen EM, McTammany ME, Webster JR, Benfield EF (2010) Shifts in allochthonous input and
 439 autochthonous production in streams along an agricultural land-use gradient. *Hydrobiologia*
 440 655:61–77. doi: 10.1007/s10750-010-0404-7
- 441 Harvey E, Gounand I, Little CJ, et al (2017) Upstream trophic structure modulates downstream
 442 community dynamics via resource subsidies. *Ecol Evol* 7:5724–5731. doi:
 443 10.1002/ece3.3144
- 444 Heiri AC, Wolf A, Rohrer L, Bugmann H (2009) Forty years of natural dynamics in Swiss beech
 445 forests: structure, composition, and the influence of former management. *Ecol Appl*
 446 19:1920–1934. doi: 10.1890/08-0516.1
- 447 Johnson S, Covich A (1997) Scales of observation of riparian forests and distributions of
 448 suspended detritus in a prairie river. *Freshw Biol* 37:163–175. doi: 10.1046/j.1365-
 449 2427.1997.00150.x
- 450 Kaelin K, Altermatt F (2016) Landscape-level predictions of diversity in river networks reveal
 451 opposing patterns for different groups of macroinvertebrates. *Aquat Ecol* 50:283–295. doi:
 452 10.1007/s10452-016-9576-1
- 453 Kominoski JS, Pringle CM, Ball BA, et al (2007) Nonadditive effects of leaf litter species
 454 diversity on breakdown dynamics in a detritus-based stream. *Ecology* 88:1167–1176. doi:
 455 10.1890/06-0674
- 456 Kominoski JS, Rosemond AD (2012) Conservation from the bottom up: forecasting effects of
 457 global change on dynamics of organic matter and management needs for river networks.

- 458 Freshw Sci 31:51–68. doi: 10.1899/10-160.1
- 459 Kuglerová L, Jansson R, Sponseller R, et al (2016) Local and regional processes determine plant
 460 species richness in a river-network metacommunity. Ecology 2:381–391. doi: 10.1890/14-
 461 0552.1
- 462 Lecerf A, Dobson M, Dang CK, Chauvet E (2005) Riparian plant species loss alters trophic
 463 dynamics in detritus-based stream ecosystems. Oecologia 146:432–442. doi:
 464 10.1007/s00442-005-0212-3
- 465 Lecerf A, Marie G, Kominoski JS, et al (2011) Incubation time, functional litter diversity, and
 466 habitat characteristics predict litter-mixing effects on decomposition. Ecology 92:160–169.
 467 doi: 10.1890/10-0315.1
- 468 Lecerf A, Richardson JS (2010) Litter decomposition can detect effects of high and moderate
 469 levels of forest disturbance on stream condition. For Ecol Manage 259:2433–2443. doi:
 470 10.1016/j.foreco.2010.03.022
- 471 Legendre P, Anderson M (1999) Distance-based redundancy analysis: Testing multispecies
 472 responses in multifactorial ecological experiments. Ecol Monogr 69:1–24. doi:
 473 10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2
- 474 LeRoy CJ, Marks JC (2006) Litter quality, stream characteristics and litter diversity influence
 475 decomposition rates and macroinvertebrates. Freshw Biol 51:605–617. doi: 10.1111/j.1365-
 476 2427.2006.01512.x
- 477 Little CJ, Altermatt F (2018a) Species turnover and invasion of dominant freshwater
 478 invertebrates alter biodiversity-ecosystem function relationship. Ecol Monogr. doi:

- 479 10.1002/ecm.1299
- 480 Little CJ, Altermatt F (2018b) Do priority effects outweigh environmental filtering in a guild of
 481 dominant freshwater macroinvertebrates? *Proceedings of the Royal Society B*. 285:
 482 20180205. doi: [10.1098/rspb.2018.0205](https://doi.org/10.1098/rspb.2018.0205)
- 483 Marcarelli AM, Baxter C V., Mineau MM, Hall RO (2011) Quantity and quality: Unifying food
 484 web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*
 485 92:1215–1225. doi: 10.1890/10-2240.1
- 486 Meyer JL, Wallace JB, Eggert SL (1998) Leaf Litter as a Source of Dissolved Organic Carbon in
 487 Streams. *Ecosystems* 1:240–249. doi: 10.1007/s100219900019
- 488 Miltner RJ, White D, Yoder C (2004) The biotic integrity of streams in urban and suburbanizing
 489 landscapes. *Landsc Urban Plan* 69:87–100. doi: 10.1016/j.landurbplan.2003.10.032
- 490 Mitchell MGE, Bennett EM, Gonzalez A (2015) Strong and nonlinear effects of fragmentation on
 491 ecosystem service provision at multiple scales. *Environ Res Lett* 10:94014. doi:
 492 10.1088/1748-9326/10/9/094014
- 493 Naiman RJ, Decamps H, Pollock M (1993) The Role of Riparian Corridors in Maintaining
 494 Regional Biodiversity. *Ecol Appl* 3:209–212. doi: 10.2307/1941822
- 495 Niyogi DK, Koren M, Arbuckle CJ, Townsend CR (2007) Longitudinal changes in biota along
 496 four New Zealand streams: Declines and improvements in stream health related to land use.
 497 *New Zeal J Mar Freshw Res* 41:63–75. doi: 10.1080/00288330709509896
- 498 Oksanen J, Blanchet FG, Kindt R, et al (2012) *vegan: Community Ecology Package*.

- 499 Orlinskiy P, Münze R, Beketov M, et al (2015) Forested headwaters mitigate pesticide effects on
500 macroinvertebrate communities in streams: Mechanisms and quantification. *Sci Total*
501 *Environ* 524–525:115–123. doi: 10.1016/j.scitotenv.2015.03.143
- 502 Peterman WE, Crawford JA, Semlitsch RD (2008) Productivity and significance of headwater
503 streams: population structure and biomass of the black-bellied salamander (*Desmognathus*
504 *quadramaculatus*). *Freshw Biol* 53:347–357. doi: 10.1111/j.1365-2427.2007.01900.x
- 505 Price B, Kienast F, Seidl I, et al (2015) Future landscapes of Switzerland: Risk areas for
506 urbanisation and land abandonment. *Appl Geogr* 57:32–41. doi:
507 10.1016/j.apgeog.2014.12.009
- 508 Rios SL, Bailey RC (2006) Relationship between riparian vegetation and stream benthic
509 communities at three spatial scales. *Hydrobiologia* 553:153–160. doi: 10.1007/s10750-005-
510 0868-z
- 511 Rosseel Y (2012) lavaan: An R Package for Structural Equation Modeling. *J Stat Softw* 48:1–36.
512 doi: 10.18637/jss.v048.i02
- 513 Ryo M, Harvey E, Robinson CT, Altermatt F (2018) Nonlinear higher order abiotic interactions
514 explain riverine biodiversity. *J Biogeogr* 628–639. doi: 10.1111/jbi.13164
- 515 Schmieder K (2004) European lake shores in danger- Concepts for a sustainable development.
516 *Limnologica* 34:3–14. doi: 10.1016/S0075-9511(04)80016-1
- 517 Snyder CD, Young JA, Vilella R, Lemarié DP (2003) Influences of upland and riparian land use
518 patterns on stream biotic integrity. *Landsc Ecol* 18:647–664. doi:
519 10.1023/B:LAND.00000004178.41511.da

- 520 Sponseller R, Benfield E, Valett M (2001) Relationships between land use, spatial scale and
521 stream macroinvertebrate communities. *Freshw Biol* 46:1409–1424. doi: 10.1046/j.1365-
522 2427.2001.00758.x
- 523 Swan CM, Gluth MA, Horne CL (2009) Leaf litter species evenness influences nonadditive
524 breakdown in a headwater stream. *Ecology* 90:1650–1658. doi: 10.1890/08-0329.1
- 525 Swan CM, Palmer MA (2006) Preferential feeding by an aquatic consumer mediates non-additive
526 decomposition of speciose leaf litter. *Oecologia* 149:107–114. doi: 10.1007/s00442-006-
527 0436-x
- 528 Sweeney BW, Newbold JD (2014) Streamside forest buffer width needed to protect stream water
529 quality, habitat, and organisms: A literature review. *J Am Water Resour Assoc* 50:560–584.
530 doi: 10.1111/jawr.12203
- 531 Swisstopo (2007) Vector 25 Gewässernetz. 5704 000 000, reproduced by permission of
532 swisstopo / JA100119, Bundesamt für Landestopographie (Art.30 Geo IV)
- 533 Swisstopo (2003) DHM 25. 5704 000 000, reproduced by permission of swisstopo / JA100119,
534 Bundesamt für Landestopographie (Art.30 Geo IV)
- 535 Swisstopo (2010) Vector 25. 5704 000 000, reproduced by permission of swisstopo / JA100119,
536 Bundesamt für Landestopographie (Art.30 Geo IV)
- 537 Vannote RL, Minshall GW, Cummins KW, et al (1980) The river continuum concept. *Can J Fish*
538 *Aquat Sci* 37:130–137. doi: 10.1139/f80-017
- 539 Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream
540 linked to terrestrial litter inputs. *Science* 277:102–104. doi: 10.1126/science.277.5322.102

- Webster JR, Covich A, Tank JL, Crockett T V. (1994) Retention of coarse organic particles in Streams in the southern Appalachian mountains. *J North Am Benthol Soc* 13:140–150. doi: 10.2307/1467233
- Webster JR, Golladay SW, Benfield EF, et al (1990) Effects of forest disturbance on particulate organic matter budgets of small streams. *J North Am Benthol Soc* 9:120–140. doi: 10.2307/1467446
- Whiting DP, Whiles MR, Stone ML (2011) Patterns of macroinvertebrate production, trophic structure, and energy flow along a tallgrass prairie stream continuum. *Limnol Oceanogr* 56:887–898. doi: 10.4319/lo.2011.56.3.0887
- Wipfli MS, Musslewhite J (2004) Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia* 520:153–163. doi: 10.1023/B:HYDR.0000027734.95586.24
- Wipfli MS, Richardson JS, Naiman RJ (2007) Ecological Linkages Between Headwaters and Downstream Ecosystems: Transport of Organic Matter, Invertebrates, and Wood Down Headwater Channels. *J Am Water Resour Assoc* 43:72–85. doi: 10.1111/j.1752-1688.2007.00007.x
- Young RG, Huryn AD (1999) Effects of land use on stream metabolism and organic matter turnover. *Ecol Appl* 9:1359–1376. doi: 10.1890/1051-0761(1999)009[1359:EOLUOS]2.0.CO;2

Figure Legends



Fig. 1 The location of the ten headwater stream catchments used in this study, on the Swiss shores of Lake Constance. Data sources: swisstopo (2017), Vector200 and TLM3D, DV 5704 000 000, reproduced by permission of swisstopo/JA100119; EEA (2011) Corine Land Cover 2000 raster data – version 15 (08/2011), European Environment Agency; ESRI © Esri Data World.

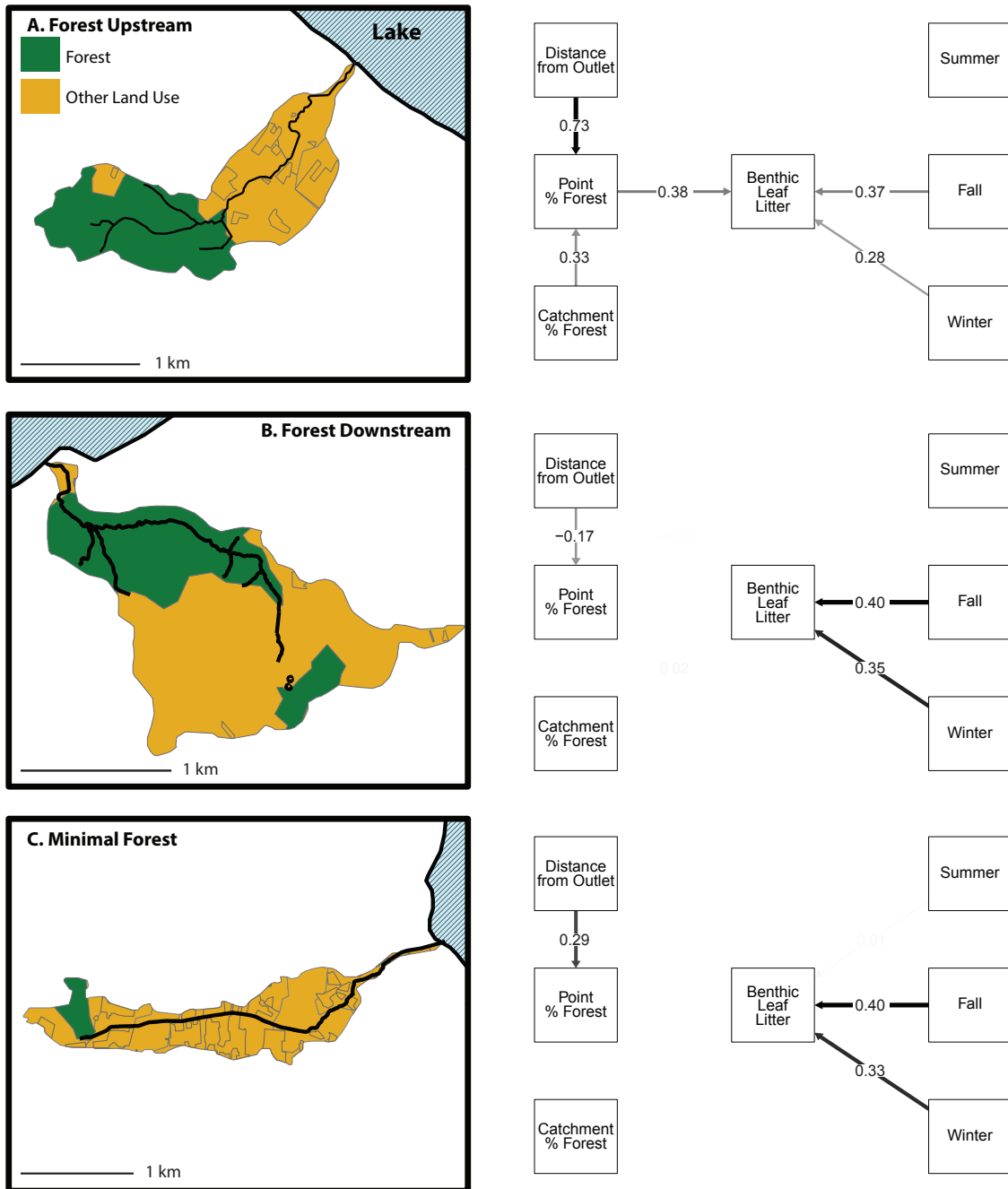


Fig. 2 Structural equation models showing sources of variation in benthic leaf litter availability in (a) catchments with forests primarily in headwaters (n=117 observations), (b) catchments with forests primarily downstream (n=138 observations), and (c) catchments with minimal forest (n=134 observations). Though we sampled three catchments of each configuration type, we only show one catchment per type as an example to help visualize the differences in land use patterns.

Only significant ($p < 0.05$) causal relationships are shown by paths in the diagrams, and color and weight of the arrows show the strength of the correlation (also indicated numerically).

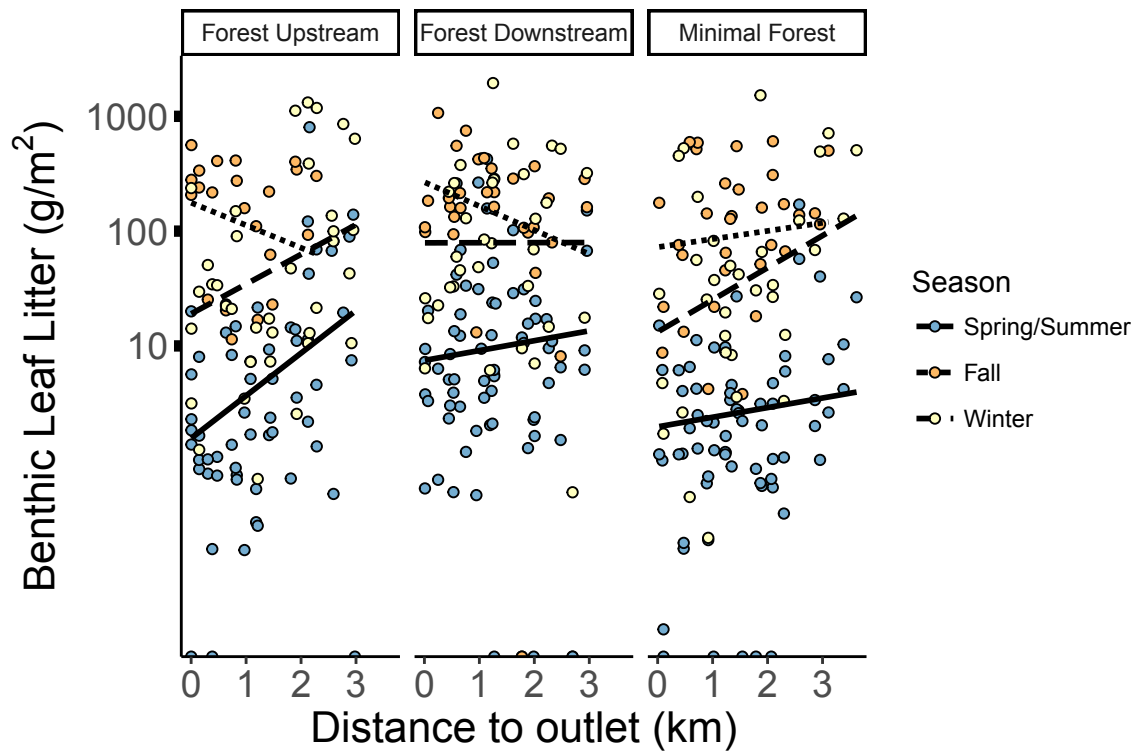


Fig. 3 Benthic leaf litter availability increased in fall and winter compared to spring and summer months across all landscape configuration types where there was a mix of forest and agriculture. The upstream distance of a point from the stream outlet into Lake Constance was indirectly associated with leaf litter availability in catchments with forest primarily upstream, but there was no relationship in catchments where forest cover was primarily in downstream areas or where there was only minimal forest cover (SEM results, see Fig. 2).

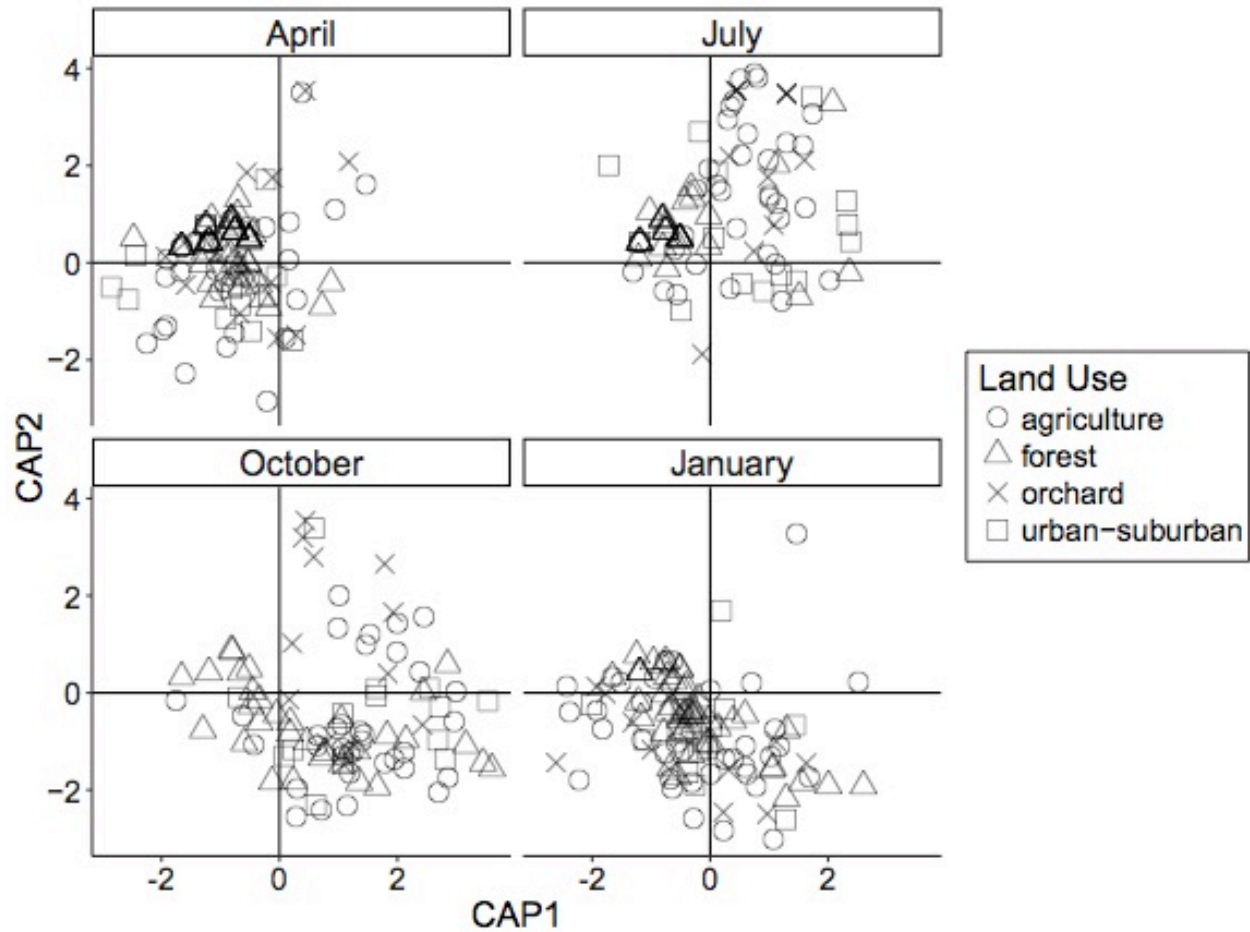


Fig. 4 Plots of the distance-based redundancy analysis (dbRDA) ordination of benthic leaf litter samples collected at each seasonal sampling point. Shapes indicate the predominant land use class in a 50-m buffer around the sampling point.

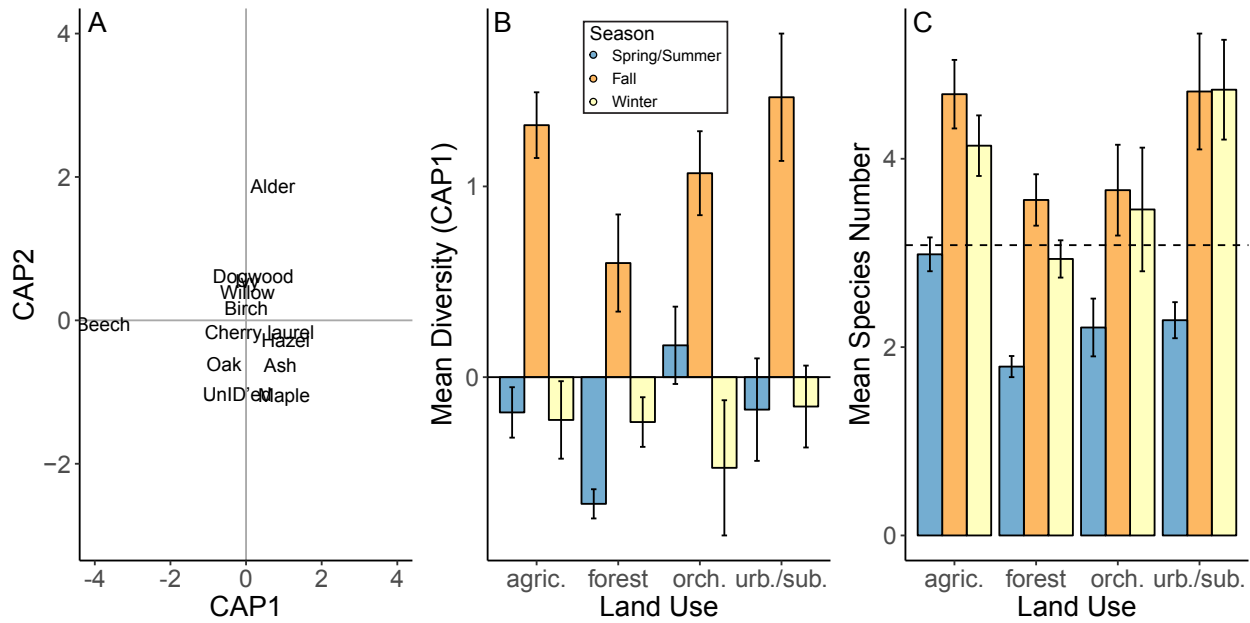


Fig. 5 (a) Loadings of tree species on the ordination axes from the distance-based redundancy analysis (dbRDA) of benthic leaf litter diversity. **(b)** Mean values of the CAP1 value from the ordination for points surrounded by different predominant land use types (agric. = agriculture, orch. = orchards and vine fruit cultivation, urb./sub. = urban, industrial, and/or suburban land use) through different seasonal sampling points. As indicated in (a), negative CAP1 values indicate dominance by beech leaves in the sample. The global mean of CAP1 values is zero. **(c)** Mean number of species present in benthic leaf litter samples by surrounding land use type and season. The global mean of species number is indicated by the dashed line. Error bars show standard error of the mean.